



Original Articles

A framework for measuring coral species-specific contribution to reef functioning in the Caribbean

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ABSTRACT

Species morpho-functional traits provide general and predictable rules to understand the dynamics of ecological communities; therefore, considering species identity is crucial in understanding ecosystem functioning. Here, we propose a framework to estimate the species-specific functional contribution of Caribbean corals according to their capacity to create complex three-dimensional structures by means of calcium carbonate precipitation and their morphological complexity. We use a combination of field data and bibliographic information to integrate a Reef Functional Index (RFI) that considers the calcification rate, structural complexity and abundance (cover) of each coral species. As an example application of this tool, we evaluated various sites along the Mesoamerican Reef showing that the RFI can be used to compare reef sites or communities. The construction capacities of Caribbean coral species are highly variable, thus, different species configurations of a coral community result in a high level of functional variation. Most coral assemblages on the Mesoamerican Reef show non-framework species dominance (e.g. *Undaria* spp. and *Porites astreoides*), compromising reef functioning. However, sites with key reef-building species present showed considerably greater functioning despite those species not being dominant. The functional approximation for coral species proposed can be used by future studies considering changes in coral community composition, keystone species loss or to estimate reef function loss due to climate change or other stressors.

1. Introduction

Assessing ecosystem functioning based on species traits provides general and predictable rules to understand community dynamics, particularly in the context of climate change and biodiversity loss (Haddad et al., 2008; Hooper et al., 2005; McGill et al., 2006); and reveals community responses to natural or anthropogenic disturbances (Mouillot et al., 2013). This is possible as the nature and magnitude of species functional traits can vary considerably (Naeem et al., 1999), and also have variable response capacity, depending on the type and intensity of pressure to which the species are subjected (Darling et al., 2013; Hooper et al., 2005; Okazaki et al., 2017; Pakeman, 2011). Therefore, while species diversity or abundance cannot reliably serve to understand the response of communities to disturbances, a functional trait-based approach can quantify, predict, and better anticipate, the impacts of disturbances on ecological communities (Mouillot et al., 2013). This is particularly important since functional traits are strongly linked to ecosystems properties, such as the role of dominant species,

keystone species, ecological engineers, and species interactions such as competition, facilitation, mutualism, disease, and predation (Hooper et al., 2005). In terrestrial ecology, patterns of ecological specialization have been reported in plants using species functional traits, as well as to explain mechanisms such as growth, survival, and reproduction (Díaz et al., 2015, 2004). In marine ecosystems, coral species functional traits have been utilized to examine global patterns of functional diversity and functional redundancy, in order to identify locations and functions where redundancy is critically lacking (McWilliam et al., 2018). This functional approach suggests that there are mechanisms of the species traits, which elucidate ecological and evolutionary processes, and the functioning of species and ecosystems.

Ecosystem structure and function are intrinsically linked to the identity of the species that create habitats (foundation species). In tropical coastal ecosystems, corals are primarily responsible for building the three-dimensional matrix that supports biodiversity and ecosystem services. In coral reefs, functioning depends, to a large extent, on coral life history strategies, which are strongly linked to species

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morphological and physiological attributes (Darling et al., 2013; Denis et al., 2017). In particular, growth rates and structural complexity define the processes of accretion and provision of habitat. Reefs dominated by species with high structural complexity and high growth rates not only maintain more diverse communities but also regulate the functional structure of ecological communities at different spatial scales (Graham and Nash, 2013; Richardson et al., 2017a,b). However, few studies recognize coral species identity and they are generally considered to be a functionally homogeneous group when assessing reef condition or conservation status (Álvarez-Filip et al., 2013; Mouillot et al., 2013; Perry et al., 2012).

The habitat-forming performance of different taxa can be approximated using a number of techniques, including the use of geometric shapes. This approach has been used for estimating phytoplankton biovolume and surface area in transitional water ecosystems (Vadrucci et al., 2013, 2007), in gorgonian and sponge ecology (Santavy et al., 2013), and in coral reef ecology and physiology (Babcock, 1991; Naumann et al., 2009; Szmant-Froelich, 1985). This approach offers important advantages as it is non-invasive and allows rapid data collection. Furthermore, geometric shapes and surface area are basic morphometric descriptors of diverse taxa communities, by which other morphometric and body-size related descriptors can be obtained (i.e. biomass, surface-to-volume ratio, length-to-width ratio, size spectra or categorization into morphological functional groups; Vadrucci et al., 2013, 2007). Recent studies propose the integration of information regarding morphology and bio-volume to estimate structural complexity and calcification rates of scleractinian coral species. Álvarez-Filip et al. (2013) estimated the calcification rate of four dominant Caribbean coral genera (*Acropora*, *Orbicella*, *Undaria*, and *Porites*) considering the morphology of each genus and assigning them to a geometric shape according to their growth form. Álvarez-Filip et al. (2013) found that calcification and structural complexity varied considerably among the four genera. *Acropora*, which forms branching structures, displayed the highest calcification rate and rugosity, while foliose *Undaria* had the lowest values. Bozec et al. (2015) used morphometric rules to describe the 3D growth of massive Caribbean corals. Santavy et al. (2013) proposed a method to quantify the ecosystem services provided by the physical structural of gorgonians and sponges of the Western Central Atlantic, based on colony morphology and measurements of colony height and diameter in the field and generation of 3D models.

Long-term changes in coral reef functioning have been most evident in the Caribbean (Gardner et al., 2003; Jackson et al., 2014). The rapid loss of coral cover has resulted in a considerable decrease in reef accretion and rugosity coral growth, calcium carbonate deposition and structural complexity (Álvarez-Filip et al., 2011, 2009; Perry et al., 2015), which seriously compromises the functional maintenance of reefs in the future (Álvarez-Filip et al., 2013; Perry et al., 2015). In addition to coral cover loss, Caribbean reefs are also experiencing a change in species composition. The few species responsible for the majority of the structural complexity have been replaced by opportunistic species (Álvarez-Filip et al., 2013, 2011; Green et al., 2008). For example, brooding reproduction species with high population turnover are generally more tolerant to environmental changes, but predominantly form small physical structures that contribute little to reef structural complexity (e.g. *Undaria* spp. and *Porites astreoides*). While branching and massive forms such as *Acropora* spp. and *Orbicella* spp., which contribute greatly to the accumulation of calcium carbonate and reef complexity, are notably less tolerant to environmental changes (Álvarez-Filip et al., 2013; Darling et al., 2013, 2012). The decline in reef structural complexity negatively affects many associated species and directly affects ecosystem processes and services essential to human well-being (Hughes et al., 2017; Jackson et al., 2014; Mumby et al., 2007; Newman et al., 2015; Richardson et al., 2017a,b).

Coral community functioning depends on three fundamental axes of each species present: (1) abundance, generally estimated as a percent

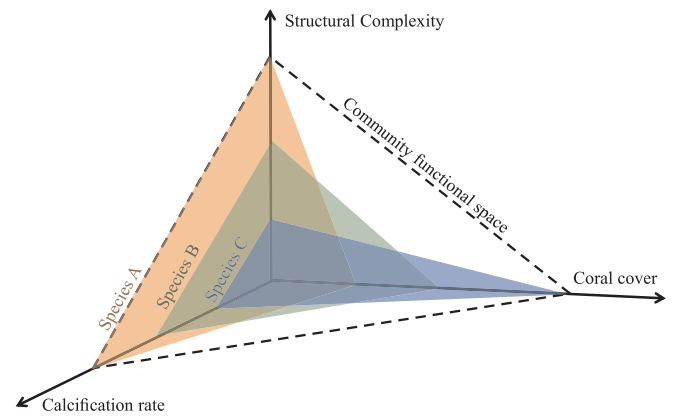


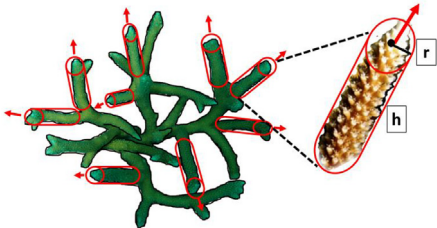
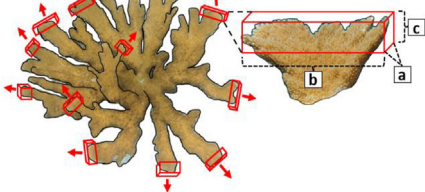
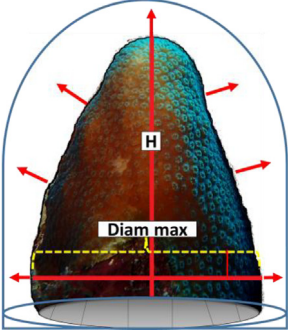
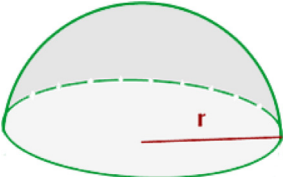
Fig. 1. Caribbean coral community functional space. Each species has three main characteristics represented by the different axes: 1) coral cover, 2) calcification rate ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) and 3) structural complexity (given by size and rugosity). Species with different levels of functionality in the ecosystem are exemplified: Individual contributions can vary naturally according to environmental conditions and human pressure (trade-offs). The combination of these three variables represents the effect of each species on the ecosystem. Community functioning is given by the integration of the individual contributions of each species. In this way, the effect of the coral community on the reef-building processes and habitat generation depend not only on the quantity of corals present but also on the traits of each species.

cover; (2) capacity to accumulate calcium carbonate (calcification rates); and (3) morphological complexity (Fig. 1). Although some protocols already consider the inclusion of species-specific information to estimate ecosystem functioning (e.g. the Reef Budget; Perry et al., 2008, 2012), they are generally based on intensive fieldwork following specific protocols, making it difficult to estimate the functional potential of sites surveyed with other methods (e.g. historical data, simplified monitoring programs used by some MPAs). Here we propose a methodology to complement the efforts made to date, through a theoretical approach based on the morphology, skeletal density and extension (calcification rates), height and rugosity (structural complexity) of each species. We use field and bibliographic data to propose a quantitative coefficient to evaluate reef-building capacity and structural complexity of the most common coral species in the Caribbean Sea. This coefficient in combination with the abundance patterns of the species present in a coral assemblage can be integrated into an index to represent the site functional potential (Fig. 1); which can easily be incorporated in other methodologies. As an example application of this tool we evaluated various sites along the Mesoamerican Reef (MAR) showing that the Reef Functional Index (RFI) can be used to compare reef sites or communities, where, depending on the coral assemblage and dominant species present, site functioning will tend towards one extreme (high or low functioning) (see Fig. 1). We expect that these results will help to better understand the functional status and condition of reefs throughout the Caribbean, as well as being used by researchers, governmental and non-governmental institutions to perform rapid assessments of coral reef condition and explore how reef functional capacity has changed over time using historical data.

2. Methods

Morphology and growth patterns were used to estimate structural complexity and calcification rates of the 47 most common scleractinian coral species reported in the Caribbean Sea. The species were selected using the ecological census databases of the Atlantic and Gulf Rapid Reef Assessment (AGRAA) (Lang et al., 2010) and Healthy Reefs Initiative (HRI) (McField and Kramer, 2007). To estimate calcification rate and structural complexity we used a combination of published

Table 1Coral species' calcification rate ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) estimation by geometric growth group. The red arrow represents the direction of colony growth.

Group	Geometric growth type	Morphometric equations to estimate calcification rate (Cr ; $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$)
Digitate	Cylindrical (e.g. <i>Acropora cervicornis</i>) 	Equation 1 Branch calcification rate: $\text{Cr} = (\pi * r^2 * h) D$ where: r = mean branch radius h = mean annual skeletal extension for each species (cm yr^{-1}) D = mean density for each species (g cm^{-3}) Equation 2 Calcification rate: Branch calcification rate * mean density of branches in a m^2
Foliose	Orthohedron (e.g. <i>Acropora nalmata</i>) 	Equation 3 Calcification rate: $\text{Cr} = (a * \Sigma b * c) D$ where: a = mean thickness of the leaf b = mean length of the leaf c = mean annual skeletal extension for each species (cm yr^{-1}) D = mean density for each species (g cm^{-3})
Massive	Paraboloid (e.g. <i>Orbicella faveolata</i>)  Hemisphere 	Equation 4 Surface Area: $\text{SA} = (\pi/6) (r/H^2) [(r^2 + 4H^2)^{3/2} - r^3]$ where: r = mean colony radius H = colony height Equation 5 Calcification rate: $\text{Cr} = ((\pi/2) (H + h) (r^2 + h) D - ((\pi/2) H r^2) D)$ where: H = mean colony height r^2 = mean colony diameter D = mean density for each species (g cm^{-3}) h = mean annual skeletal extension for each species (cm yr^{-1}) Equation 6 Calcification rate: $\text{Cr} = ((2/3) (\pi * (r^3 + h))) D - ((2/3) (\pi * r^3)) D$ where: r = mean colony radius (m) D = mean density for each species (g cm^{-3}) h = mean annual skeletal extension for each specie (cm yr^{-1})

literature (coral growth and skeletal density) and fieldwork (morphometric data).

2.1. Calcification rate

Coral growth can be described by the extension rate (cm yr^{-1}) and skeletal density (g cm^{-3}) of the coral skeleton and the calcification rate determined as the product of these two variables (Carricart-Ganivet, 2011; Carricart-Ganivet et al., 2000; Dodge and Brass, 1984). However, this does not consider how calcification varies according to different coral morphologies. In this study, we evaluated the calcification rate for each species based on information regarding morphological attributes, in order to avoid overestimation of calcium carbonate production for structurally complex colonies and better represent the contribution of habitat-forming species to reef accretion (Alvarez-Filip et al., 2013; Bozec et al., 2015). In addition to density and extension rates, species were grouped according to growth and morphology: 1) cylindrical growth (branching and digitate morphology); 2) orthohedron growth (e.g. foliose); and 3) paraboloid and hemispheric growth (massive) (Table 1).

We used data from published literature on extension rate (cm yr^{-1}) and skeletal density (g cm^{-3}) for each species obtained from the Reef Budget online database (Perry et al., 2012) and complemented this with other published literature (Table S1). Quantitative morphometric data for the different species were collected in the field between October 2015 and May 2016 throughout the Mexican Caribbean, from various reef zones and types. The number of colonies measured depended on species abundance, although in many cases sampling was focussed on certain rare species to complement existing data. When it was not possible to obtain morphometric data in the field, we used data for the closest related species or group available as a proxy, prioritizing morphological similarity (Table S2). Furthermore, if more than two species were used as a proxy, the average value of those species was adopted (e.g. the value for *Acropora prolifera* is equal to the average between *A. cervicornis* and *A. palmata*; Table S2).

Morphometric data was taken in the field to estimate calcification rates of branching and digitate coral species. For each colony, approximately 20% of branches were selected randomly from all parts of the colony. The diameter of each branch was measured at the distance from the tip of the branch equal to the mean annual skeletal extension

rate of the species (to consider a year of growth along the axis of maximum extension; e.g., *A. cervicornis* at $\sim 10 \text{ cm yr}^{-1}$, see Table S2). Mean branch diameter was then determined for each colony and species. Photographs were taken of the apical part of colonies and subsequently analyzed with ImageJ v2.1.4.7 software to estimate the area occupied by the colony (planar view from above) and quantify the number of branches per colony. The number of branches per colony was averaged per species, and mean branch density per m^2 determined. The geometric growth pattern of branching species tends to be cylindrical, so the calcification rate of each species was calculated per branch using Eq. (1) (Table 1). Subsequently, using Eq. (2) branch calcification rate was multiplied by mean branch density for each species to determine the mean calcification rate for each branching species (Table 1).

Field data (Table S2) was also used for foliose-shape species. The thickness of the foliose areas of each colony was measured at the distance from the top of the leaf equal to the mean annual skeletal extension rate of the species (to consider a year of growth along the axis of maximum extension; e.g. *Millepora complanata* at $\sim 1.6 \text{ cm yr}^{-1}$). Photographs were taken, and ImageJ software used to estimate the length of each leaf in the colony. Lengths were then added to have a 'total leaf length for the colony' (Table 1). For the species *Undaria tenuifolia*, $25 \times 25 \text{ cm}$ quadrants were used as the high density of leaves is difficult to quantify. The geometrical growth pattern of the foliose and package-shaped species tends to be orthohedron, and consequently calcification rate for each species was estimated using Eq. (3) (Table 1).

Massive growth forms were classified into two sub-groups: i) paraboloid, for which data were obtained in the field; and ii) hemispheric, for which no field data were obtained (Table S2) as they are rare species and were not encountered during sampling. For paraboloid species, the diameter of the maximum axis and height of each colony was measured, and species mean values determined. The surface area of one colony was estimated to 1 m^2 using the average ratio of height and diameter (Eq. (4), Table 1). Using this information, species calcification rate was estimated based on the annual volume of paraboloid growth, based on annual skeletal extension (Eq. (5), Table 1). For massive species without field information, we adopted the methodology of Álvarez-Filip et al. (2013), where calcification rate was calculated as the difference in how much calcium carbonate a hemisphere accumulates in a year with a basal area of 1 m^2 . Which is given by the difference of the extension rate (cm yr^{-1}) of each species (Eq. (6), Table 1). A value of the calcification rate was obtained for each species.

2.2. Structural complexity

Colony-level structural complexity was determined based on the colony rugosity index (Álvarez-Filip et al., 2011; Bozec et al., 2015) and maximum colony height. The rugosity index is the ratio of the length of the contour from the beginning to the end of the colony to the linear distance along the maximum colony axis. A totally flat colony has a rugosity index of 1 while higher values indicate greater complexity. The rugosity and height of 562 coral colonies were measured in Cozumel (in 2009 and 2015), Puerto Morelos (in 2012 and 2015) and Sian Ka'an (in 2016) within a depth range of 2–19 m. Subsequently, the rugosity index and height of all colonies were averaged per species. Species structural complexity was calculated as the product of mean rugosity index and mean colony height. For species where field information was not obtained, the value of the closest related species or morphological group was adopted.

2.3. Reef functional index for Caribbean coral communities

An RFI is proposed considering the morpho-functional attributes of each species. The index focuses on quantifying the relative contribution of abundance (live coral cover) of the species present in a coral reef system

by integrating mean calcification rate, rugosity, and height of each species. First, variables were scaled using the minimum and maximum value of each variable as: $X = (x - \text{min value}) / (\text{max value} - \text{min value})$, where x is the value of calcification rate, rugosity and colony height of each species (see Table 2). This standardization allows variables to have differing means and standard deviations but equal ranges (0–1). Subsequently, a species-specific Functional coefficient (F_c) was obtained by averaging the standardized values of each of the three metrics (Table 2).

The RFI is obtained through the summation of the product of abundance (live coral cover) and the F_c of each species for the study site, through the following equation: $\sum ((Lcc_i/100)(F_{c_i}))$, where: Lcc_i is the percentage of live coral cover for each species and F_{c_i} the Functional coefficient for each species (i). To ease interpretation RFI is then fourth root transformed to facilitate numerical interpretation. A value close to 1 represents dominance of species with the highest calcification rates and the highest values of structural complexity. A theoretical site with 100% coverage of *Acropora palmata* (the Caribbean species with the highest calcification rate and complexity) would have an RFI of 0.97.

With species estimates of calcification rate and structural complexity, the functional potential of coral species in the Caribbean was explored through a Principal Components Analysis (PCA). This analysis allows the identification of patterns in the data and the recognition of similarities and differences in calcification, rugosity, and height variables. The analyses were carried out with R version 3.4.1. using the ggplot2 and Factoextra packages (Kassambara and Mundt, 2017; Wickham and Chang, 2015).

2.4. Functional potential of coral communities in the Mesoamerican Reef

To evaluate the functioning of MAR coral communities, species-level live coral cover data collected by HRI between August 2010 and November 2014 were used. A total of 170 sites were included, of which 37 were located in Mexico, 10 in Guatemala, 40 in Belize and 83 in Honduras (accessible online through AGRRA and HRI). In the cases where data were available for the same site in different years, only the most recent data were used.

The methods used by HRI to collect information on ecological indicators are detailed below. Site selection was based on benthic habitat maps produced by the Millennium Reef Mapping Program, with $200 \times 200 \text{ m}$ sites randomly selected using geographic information systems, following stratification by geomorphological characteristics and depth (Andréfouët et al., 2003; Lang et al., 2010). At each reef site, between six and ten 10 m lines transects, separated by at least 5 m, were haphazardly deployed on the reef, parallel to the coast. For each site, substrate cover of all benthic components was recorded, following AGRRA point intercept methodology (Lang et al., 2010).

We used the Natural Breaks algorithm (Jenks, 1967) to compare reef site RFI and live coral cover, which groups data according to the inherent breaks present. The algorithm looks for the points where the difference in the data (sites) is maximized, and it uses those points to delimit each class or group. This method calculates the differences in the values between the sites ordered in ascending value. It then sets a limit to separate the groups where the differences in value are highest. The analyses were done with R version 3.4.1. and QGIS software version 2.18.12.

The relationship between coral cover and the RFI was explored for the sites dominated by the most abundant Caribbean coral genera (*Acropora*, *Orbicella*, *Porites*, and *Undaria*). Genera or morphological groups were classified as dominant if they exhibited more than 50% cover of a site. The analyses were carried out with the R version 3.4.1. using the ggplot2 package (Wickham and Chang, 2015).

Table 2

Mean coral species calcification rate ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), rugosity index and height (cm), considering colony morphology. The Functional coefficient (Fc) is the average of the three previously standardized metrics (see methods). S.D. = Standard Deviation. The * indicates that data of the closest morphological (or taxonomic) species were used, due to lack of data for the species (see Table S2).

Species	Morphology	Mean calcification rate ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$)	Mean rugosity	S.D.	Mean colony height (cm)	S.D.	Fc
<i>Acropora cervicornis</i>	Branching	19.28	2.27	0.59	32.00	10.37	0.623
<i>Acropora palmata</i>	Branching	17.94	3.66	1.27	80.27	44.42	0.977
<i>Acropora prolifera</i>	Branching	9.41	2.97	*	56.14	*	0.640
<i>Agaricia fragilis</i>	Foliose	0.10	1.55	*	11.96	*	0.115
<i>Agaricia lamarcki</i>	Foliose	0.09	1.27	*	11.96	*	0.081
<i>Colpophyllia natans</i>	Massive	4.47	1.45	0.18	31.85	33.57	0.263
<i>Dendrogyra cylindrus</i>	Massive	12.13	1.84	*	38.95	*	0.474
<i>Dichocoenia stokesii</i>	Massive	4.09	1.51	0.38	7.33	4.03	0.160
<i>Diploria labyrinthiformis</i>	Massive	5.86	1.61	0.20	27.67	11.94	0.289
<i>Eusmilia fastigiata</i>	Massive	8.19	1.53	0.30	7.23	4.88	0.233
<i>Favia fragum</i>	Massive	7.83	1.25	*	3.82	*	0.178
<i>Helioseris cucullata</i>	Foliose	0.09	1.08	0.04	4.25	3.86	0.024
<i>Isophyllia rigida</i>	Massive	3.76	1.32	0.17	6.30	3.75	0.126
<i>Isophyllia sinuosa</i>	Massive	3.57	1.16	0.12	3.17	3.14	0.089
<i>Madracis auretenra</i>	Digitate	4.86	1.44	0.20	8.58	4.83	0.170
<i>Madracis decactis</i>	Digitate	13.70	2.03	1.04	9.86	11.87	0.403
<i>Madracis formosa</i>	Digitate	9.28	1.40	*	9.22	*	0.245
<i>Manicina areolata</i>	Massive	11.74	1.13	One colony	2.00	One colony	0.222
<i>Meandrina jacksoni</i>	Massive	1.53	1.29	1.13	35.50	34.65	0.206
<i>Meandrina meandrites</i>	Massive	1.93	1.35	0.26	11.82	15.93	0.121
<i>Millepora alcicornis</i>	Digitate	0.65	2.19	0.69	10.00	8.38	0.197
<i>Millepora complanata</i>	Foliose	5.01	1.65	0.76	8.58	12.36	0.200
<i>Millepora squarrosa</i>	Foliose	3.33	1.91	*	9.29	*	0.205
<i>Millepora striata</i>	Foliose	3.33	1.91	*	9.29	*	0.205
<i>Montastrea cavernosa</i>	Massive	6.62	1.86	0.49	28.00	20.99	0.334
<i>Mussa angulosa</i>	Massive	4.28	1.27	*	3.23	*	0.117
<i>Mycetophyllia aliciae</i>	Foliose	0.08	1.37	0.23	3.33	1.63	0.057
<i>Mycetophyllia ferox</i>	Foliose	0.08	1.03	0.05	2.50	0.71	0.010
<i>Mycetophyllia lamarckiana</i>	Foliose	0.08	1.22	0.13	3.86	3.24	0.040
<i>Orbicella annularis</i>	Massive	10.71	1.89	0.34	43.44	23.90	0.474
<i>Orbicella faveolata</i>	Massive	11.49	1.91	0.48	34.46	24.99	0.453
<i>Orbicella franksi</i>	Massive	9.20	1.90	*	38.95	*	0.431
<i>Porites astreoides</i>	Massive	5.78	1.54	0.43	8.59	7.32	0.199
<i>Porites divaricata</i>	Digitate	1.45	1.41	0.13	11.75	5.32	0.120
<i>Porites furcata</i>	Digitate	1.86	1.39	0.02	9.00	1.41	0.113
<i>Porites porites</i>	Digitate	5.15	1.77	0.39	11.70	5.22	0.230
<i>Pseudodiploria clivosa</i>	Massive	5.13	1.70	0.40	19.36	6.96	0.252
<i>Pseudodiploria strigosa</i>	Massive	5.23	1.87	0.53	24.76	17.08	0.299
<i>Scolymia cubensis</i>	Massive	4.28	1.25	*	3.23	*	0.114
<i>Scolymia lacera</i>	Massive	4.28	1.25	*	3.23	*	0.114
<i>Siderastrea radians</i>	Massive	2.85	1.03	0.06	1.20	0.57	0.053
<i>Siderastrea siderea</i>	Massive	6.51	1.35	0.26	11.71	9.84	0.201
<i>Solenastrea bournoni</i>	Massive	14.08	1.11	One colony	10.00	One colony	0.294
<i>Stephanocoenia intersepta</i>	Massive	4.05	1.09	0.13	1.75	1.77	0.084
<i>Undaria agaricites</i>	Massive	4.27	1.51	0.42	10.23	7.63	0.175
<i>Undaria humilis</i>	Massive	5.28	1.00	0.00	1.00	0.00	0.090
<i>Undaria tenuifolia</i>	Foliose	0.86	1.83	0.52	24.67	13.67	0.218

3. Results

3.1. Calcification rate and structural complexity

A total of 47 reef-building coral species from 25 genera were recorded, including four species of calcareous hydrocoral of the genus *Millepora*. The species were classified according to their morphology: 3 branching species, 7 digitate, 27 massive, and 10 foliose (Table 2).

Calcification rate varied by coral species and morphology, and ranged between 0.08 and $19.28 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$. *Acropora palmata* and *A. cervicornis* (branching) presented the highest calcification rates, followed by *Solenastrea bournoni* (massive) and *Madracis decactis* (digitate, Table 2). Rugosity index varied between species and morphology, ranging from 1 to 3.66. Species of the genus *Acropora* (branching) contributed most to rugosity (Table 2), followed by *M. decactis* (digitate). Average height varied considerably between species and morphology, and ranged between 1 and 80.27 cm. *A. palmata* and *A. prolifera* (branching) displayed the greatest mean height, with other tall species including *Orbicella* spp., *Dendrogyra cylindrus* and *Meandrina*

jacksoni (all massive, Table 2). The Functional coefficient (Fc) was greatest for the branching *Acropora* spp. and lowest for the foliose *Mycetophyllia* spp. (Table 2).

3.2. Caribbean coral species functional potential

The principal components analysis shows the similarity between species quantitatively according to calcification rate and structural complexity (rugosity and height, Fig. 2). Structural complexity was mostly correlated to principal component 1, which explained 75.4% of the variance. Calcification rate was mostly correlated to component 2, which explained 18.4% of the variance. In total, 93.8% of the functional variance is explained between the two main axes. The species that presented a greater correlation to structural complexity were *Acropora* spp. (branching), some massive species such as *Orbicella* spp. and *D. labyrinthiformis* (Fig. 2). The species that most correlated with calcification rate were *A. cervicornis* (branching), *Solenastrea bournoni*, *Manicina areolata*, *Madracis decactis* (Fig. 2). The remaining digitate and massive species did not have a strong correlation with any of the three

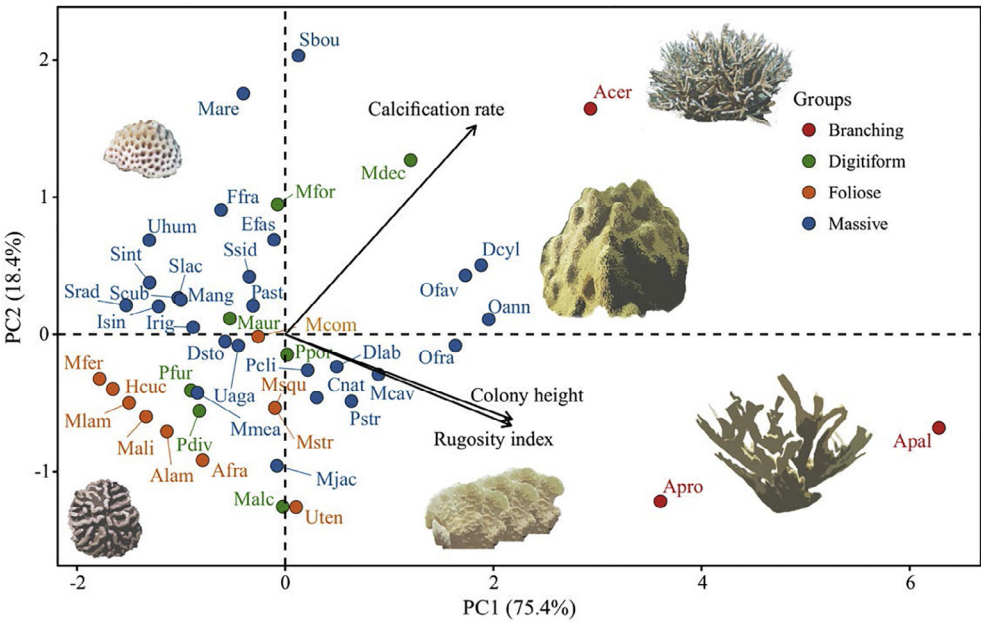


Fig. 2. Caribbean coral species functional space in relation to species calcification, rugosity, and mean height. The two main axes of a principal components analysis are presented, where component 1 represents structural complexity (rugosity and height) and component 2 calcification rate. Point colour indicates morphology: foliose (yellow), massive (blue), digitate (green) and branching (red). Species codes are given in Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

variables (Fig. 2). Foliose species also did not have an obvious correlation with any of the three variables (Fig. 2), which means that they have a lesser contribution to reef-building potential.

3.3. Mesoamerican Reef coral community functional status

On the MAR most coral species contribute little to site-level reef-building potential, including *Porites astreoides*, *U. agaricites*, *Siderastrea siderea* and the widely abundant *Undaria tenuifolia* (that despite its low calcification rate provides considerable structural complexity). Together, these four-species account for 49.6% of the relative abundance of the species present on the MAR. Conversely, species that have high functional potential such as *Orbicella* spp. and *Acropora* spp. had low relative abundance (11.6% and 8.8%, respectively) and distribution (Fig. 3). *Orbicella* only appears with coral cover > 9% in seven sites, and *Acropora* in nine sites.

Sites with higher coral cover tend to exhibit greater reef functioning, however, as coral cover increases so does variance in RFI. This variance is mainly explained by the identity of the dominant genus

present (Fig. 4). Sites dominated by *Undaria* spp. and *Porites* spp. exhibited a low level of functioning, even if they had high coral cover (> 50%). Conversely, sites dominated by *Acropora* spp. showed the highest level of functioning, above the average RFI of all sites (Fig. 4). Sites dominated by *Orbicella* showed a greater increase in the level of functioning as live coral cover increased compared to other sites; however, no sites with greater than 25% *Orbicella* coral cover were encountered. Some sites dominated by weedy species displayed a high RFI; however, this was due to sufficient abundance of key reef-building species. For example, a site located in Honduras dominated by *Porites* exhibited a very high level of functioning due to *Acropora* cover greater than 9% (Fig. 5).

We classified the 170 Mesoamerican Reef sites into five categories according to coral cover and RFI (see Methods): Outstanding, Stable, Susceptible, Impaired and Poor (Fig. 5). Although the number of sites in each category was relatively similar for both metrics (Fig. 5), 30% of sites ranked differently using coral cover or RFI, and most of these sites were in the Outstanding and Stable categories. For example, only three sites (out of ten) ranked as ‘Outstanding’ in the coral cover and RFI

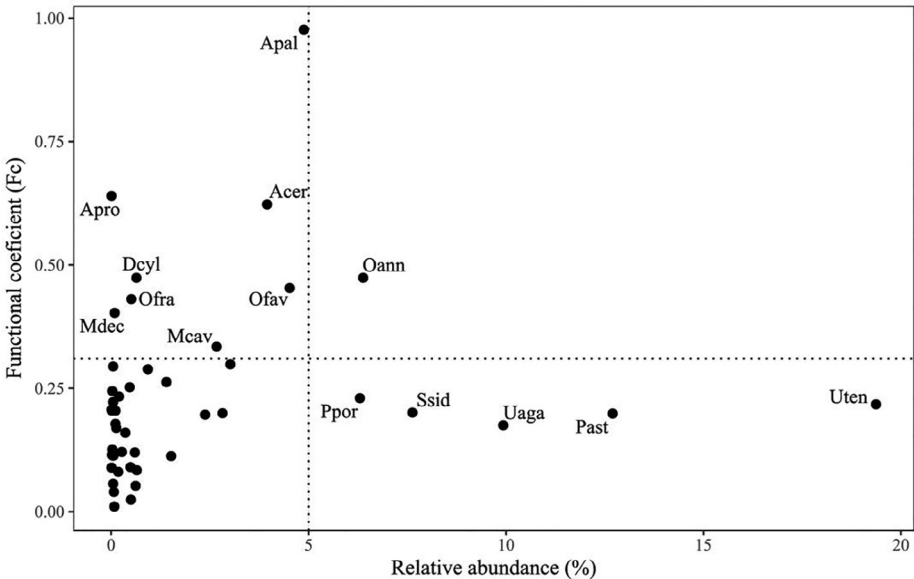


Fig. 3. Relationship between species relative abundance (%), and Functional coefficient (Fc) across 170 sites surveyed on the Mesoamerican Reef between 2010 and 2014. Dashed vertical lines highlight species with more than 5% relative abundance, and dashed horizontal lines highlight species with Fc greater than 0.3 Fc. To show the high variation in RFI and facilitate visual interpretation, the RFI was not fourth root transformed. Species codes are given in Table S1.

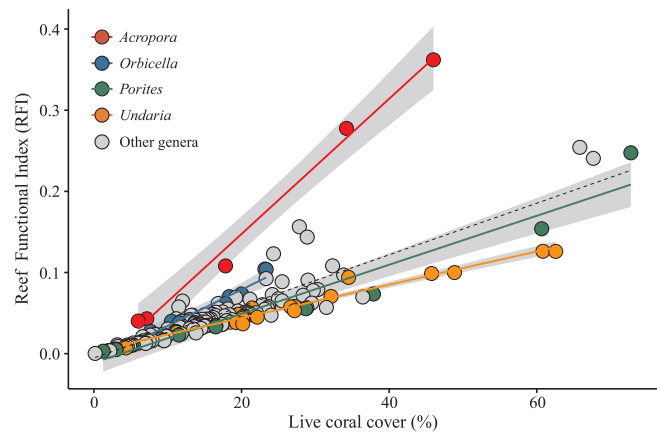


Fig. 4. Relationship between live coral cover and the Reef Functional Index for 170 sites on the Mesoamerican Reef. Colors indicate sites dominated by *Acropora* (Red), *Orbicella* (Blue), *Porites* (Green), *Undaria* (Orange), and other genera (Black). The dashed line is the regression line of best fit for all sites. The linear regressions with 95% confidence intervals for sites dominated by the four most common coral genera are also shown and the relationships are as follows: *Acropora*; ($y = 0.007x$; $R^2 = 0.994$; $P < 0.001$), *Orbicella* ($y = 0.003x$; $R^2 = 0.989$; $P < 0.001$), *Porites* ($y = 0.002x$; $R^2 = 0.955$; $P < 0.001$), *Undaria* ($y = 0.002x$; $R^2 = 0.991$; $P < 0.001$). To show the high variation in RFI and facilitate visual interpretation, the RFI was not fourth root transformed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

classification, while only five sites (out of 23) ranked as ‘Stable’ in both categories. Most of the sites that fall in the same category for both coral cover and RFI were those in the low-end categories (‘Impaired’ and ‘Poor’) as they have consistently low coral cover and were mostly dominated by non-framework building corals (see Fig. 4).

4. Discussion

Coral species traits are key to understanding reef ecosystem functioning (Darling et al., 2012; Denis et al., 2017; Edinger and Risk, 2000; McWilliam et al., 2018; Murdoch, 2007). Here, we propose a methodology to estimate the species-specific functional contribution of Caribbean corals according to their capacity to construct complex three-dimensional structures by means of calcium carbonate precipitation. This method considers species functional identity driven by species morphological and physiological attributes. The results show high variation between the construction capacities of Caribbean reef species. Thus, different species configurations in a coral community result in a high level of functional variation. Usually, the status of a reef site is principally evaluated with coral cover; but this is an incomplete representation of reef condition and functioning. Using the methodology presented here, site functioning is determined by the composition of coral assemblage and the dominance patterns of reef-building keystone species, and can be used to functionally compare any coral configuration in the Caribbean (Fig. 2).

Our findings show a clear variation in the capacity of different coral species to contribute to reef functioning, which is related to the variation in coral morpho-functional attributes used to estimate species functionality. Our findings suggest that species identity is a key factor in reef-building potential. For example, species of the genus *Acropora* contribute most to reef functioning, due to high calcification rates and the formation of complex three-dimensional structures. Other species that contribute substantially to reef functioning are *Orbicella* spp., as well *Dendrogya cylindrus* and *Solenastrea bournoni* (although these last two species are uncommon in most of the Caribbean). The species that least contributed to reef-building included those of the genera *Undaria*, *Agaricia*, *Mycetophyllia* and *Siderastrea*, in addition to other generally small massive-form species (Table 2). These findings coincide with Álvarez-Filip et al. (2013, 2011; Darling et al. (2012); Denis et al. (2017); and Edinger and Risk, (2000), which suggest that coral morphology and life history influence the degree of reef functioning.

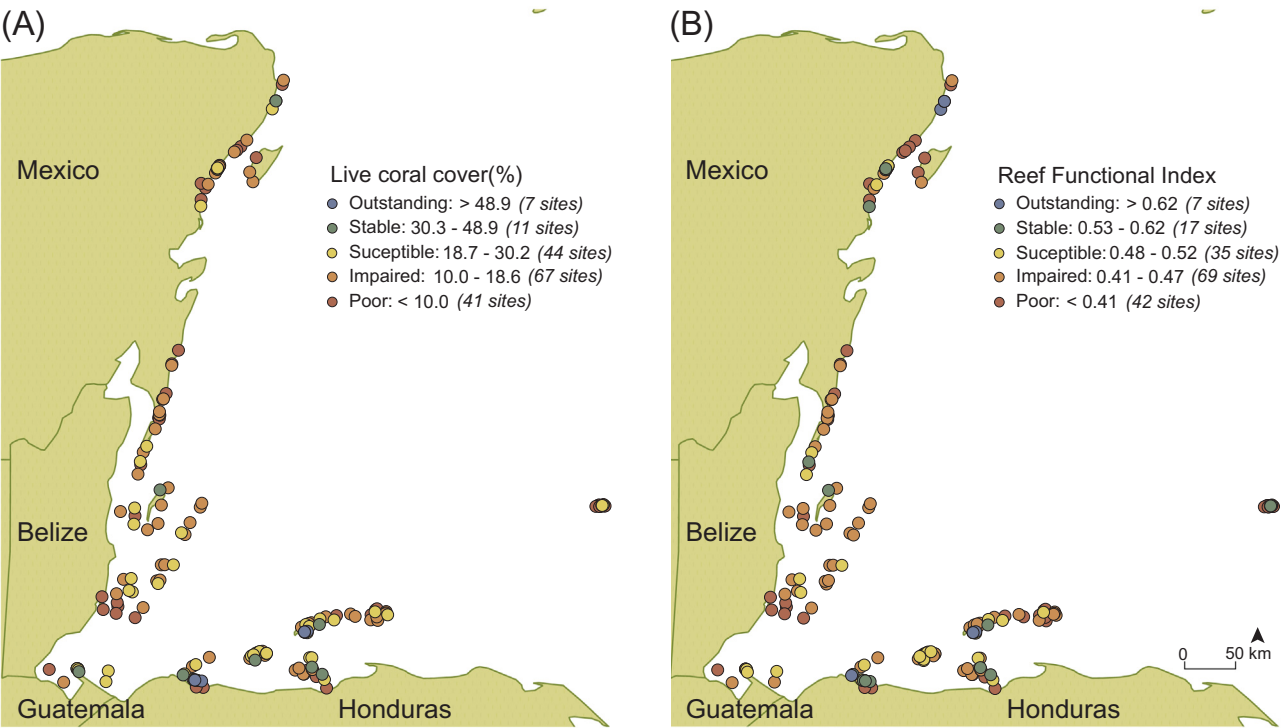


Fig. 5. Comparative map of sites along the Mesoamerican Reef, where: a) shows live coral cover, and b) shows the RFI. Site colours show the level of each indicator according to the natural breaks algorithm (see methods). The number of sites in each category is shown in parentheses.

In terrestrial ecology, there is ample evidence on how the traits of different plant species regulate terrestrial ecosystem functioning, suggesting that there are different life history strategies according to the environmental conditions to which species are adapted (Grime, 1977; Grime and Pierce, 2012; Steffen, 1996). For coral reefs, the evaluation of species' contribution to reef building is important in order to identify keystone species, which can maintain the processes and properties of the ecosystem (Díaz et al., 2015, 2004; Hooper et al., 2005). In this study, we identified species, which tend to one end of the functional spectrum (e.g., greater functional species: *Acropora* spp and *Orbicella* spp.; and lesser functional species *Undaria* spp., *Mycetophyllia* spp. and *Porites* spp.) which can serve to judge the functional level of other species or coral community configurations based on their morpho-functional traits (e.g., McWilliam et al., 2018). It is important to note that species (both on land or in the ocean) respond to multiple factors in different ways to those explored here, through a wide range of characteristics, related to specific biotic and abiotic conditions in their habitat (Díaz et al., 2015).

Coral community functioning depends on the traits of the species involved, as well as the environmental factors that determine its ecological performance (Carricart-Ganivet et al., 2012; Darling et al., 2013; Rachello-Dolmen and Cleary, 2007). No environmental gradients were considered in our models, as our main objective was to theoretically assess the general functional potential of different species at an individual and community level. However, we acknowledge that species' ecological niche differs under different environmental conditions (Baker and Weber, 1975; Graus and Macintyre, 1982 Carricart-Ganivet et al., 2007; Todd, 2008), and consequently the functional contribution of coral species and communities depends on the physical and chemical properties of the environment. Intra-specific morphological changes (polymorphism) have been reported for corals as part of adaptations to improve efficiency under varying environmental conditions (Chappel, 1980; Hoogenboom et al., 2008; Muko et al., 2000; Todd, 2008). Coral calcification rate is light dependant, and may be affected by other factors such as wave stress and sediment flux (Chappel, 1980). For example, under high light intensity conditions massive and submassive corals are hemispherical, while at low light levels colonies have a plate morphology as skeletal extension decreases and skeletal density increases (Graus and Macintyre, 1982, 1976; Bosscher, 1993). Patterns of coral growth also exhibit high morphological plasticity in response to variations in water movement (Todd, 2008). For example, in the Indo-Pacific *Acropora aspera* colonies are denser in environments more exposed to wave energy, and show reduced corallite features (Brown et al., 1985). Furthermore, nutrient gradients play an important role in the morphogenesis of branching corals with an accretive growth process (Kaandorp et al., 2005). Our functional estimates (Fc and RFI) are easily stratified to coral communities under differing environmental conditions; for example, shallow and deep reefs as new morphometric information from certain habitats (e.g., deep reefs) become available.

Functional redundancy in coral reefs can be evaluated with species traits (McWilliam et al., 2018); these traits are related to species distribution according to environmental gradients. These gradients will also affect the coral configurations present. For example, *A. palmata* is predominantly restricted to reef crests and shallow depths (Goreau, 1959), and therefore will only contribute to reef functioning there. The loss of *A. palmata* has compromised reef functioning due to low functional redundancy of Caribbean reef crests since there are no species that contribute to functioning to the same extent (e.g., *Millepora complanata*). Massive species that can be found in the same coral assemblage such as *Colpophyllia natans*, *Pseudodiploria* spp. and *Montastrea cavernosa* play a very similar functional role due to their morpho-functional traits. Because of these similar functional roles, the functional niche of this group will be more resilient to the loss of any one species (McWilliam et al., 2018; Rosenfeld, 2002).

Our results show a very broad spectrum of species functionality (Fig. 2). This spectrum could be promoting a wide diversity of

associations with invertebrates and resident fishes due to multiple levels of complexity (and scales) provided by the ecosystem (Agudo-Adriani et al., 2016; Darling et al., 2017; Graham and Nash, 2013; Richardson et al., 2017a,b). This structural complexity can be explained by coral morphology or colony complexity. Coral communities with a high RFI, generally dominated by *Acropora* and *Orbicella*, are providing a certain type of structural habitat. While communities with a lower RFI, dominated by *Undaria*, *Porites* and *Siderastrea* provide a different type of habitat. Consequently, coral diversity could influence the composition of the associated biotic community (Gratwicke and Speight, 2005; Newman et al., 2006). For example, *A. cervicornis* forms monospecific patches of varying sizes, providing refuge from predation between its branches for related assemblages of fishes and other taxa (Agudo-Adriani et al., 2016). Furthermore, high structural complexity (high RFI) strongly influences abundance, biomass, diversity, richness and trophic structure of fish assemblages (Darling et al., 2017; Gratwicke and Speight, 2005).

Our coral species composition analysis for the MAR showed that most species contribute little to site-level reef-building potential, such as the widely abundant *Undaria* spp. and *Porites* spp. Together, these genera account for nearly 50% of the relative abundance of coral species present in the entire MAR region. Conversely, species that have high functioning potential such as *Orbicella* and *Acropora* have limited relative abundance (11.62% and 8.83%, respectively) and distribution (Fig. 3). *Orbicella* only appears with coral cover greater than 9% in seven sites, and *Acropora* in nine sites. These results coincide with several studies that have highlighted that non-framework (weedy) species are rapidly increasing their relative abundance in the Caribbean (Alvarez-Filip et al., 2011; Green et al., 2008; Jackson et al., 2014; Perry et al., 2015). Consequently, there are now very few sites that are dominated by key reef-building species and reef functioning has diminished region-wide. Rodríguez-Martínez et al. (2014) found limited abundance of *A. palmata* throughout the MAR, and that it is highly dominant only in the Limones site, north of Quintana Roo, Mexico. Furthermore, *Orbicella* spp. have shown a reduction in their populations in the Caribbean due to disease and biotic effects (Bruckner and Bruckner, 2006; Edmunds and Elahi, 2007). The increasing dominance of weedy species has serious consequences for reef functioning, fisheries sustainability, coastal protection and adaptability to climate change (Bellwood et al., 2004; Hoegh-Guldberg et al., 2007; Kennedy et al., 2013).

Reef functioning increases with coral cover, but the magnitude of functional increase depends on the composition and dominance patterns of key groups in the reef. A strong correlation between RFI and live coral cover was identified for 170 sites along the MAR (Fig. 4). *Acropora* dominated sites which displayed greater functioning, where calcification rates and structural complexity increased with coral cover. Sites where *Acropora* spp. and *Orbicella* spp. displayed greater than 9% cover had considerably greater functioning despite those species not being dominant, highlighting the ecological importance of these reef-building species in maintaining reef function. If the populations of these key reef-building species continue to decline, the functioning of the entire region will be compromised in the future, with negative calcium carbonate budgets and low structural complexity (Alvarez-Filip et al., 2013; Perry et al., 2013). However, it is important to identify sites where there is still a reasonable abundance of key reef-building species before there is a transition to non-framework building species. Similarly, we can assume that the species diversity in a site needs to be treated with caution when evaluating the functional status of the reef since this is not directly related to an increase in reef complexity or accretion (Johnson et al., 2008). However, coral diversity could be influencing other processes, for example, the capacity to respond to anthropogenic disturbances or effects of climate change (Okazaki et al., 2017).

In this study we have presented a novel methodological approach to evaluate the contribution of Caribbean coral species to reef functioning.

This methodology can be used during reef condition evaluation to complement commonly employed indicators such as coral cover (Díaz-Pérez et al., 2016; McField and Kramer, 2007). The methodology can also be used to assess the functional impact of changes in coral community composition such as the loss of certain keystone species and to estimate reef functioning trajectories in response to stressors such as climate change (Álvarez-Filip et al., 2013; Bozec et al., 2015; Darling et al., 2013; Kennedy et al., 2013; Okazaki et al., 2017). The information and index presented here would greatly benefit with future studies aiming to produce species-level estimates of calcification rates and structural complexity under different environmental conditions, especially in the case of uncommon or rare species.

5. Competing interests

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolind.2018.08.038>. These data include Google maps of the most important areas described in this article.

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